Dynamics of Interacting Elk Populations Within and Adjacent to Rocky Mountain National Park

By

Bruce C. Lubow[1]
Francis J. Singer[2]
Therese L. Johnson[3]
David C. Bowden[4]

Abstract. We studied population subdivision and density dependent and independent factors influencing population processes between 1965–2001 for elk (*Cervus elaphus*) inhabiting Rocky Mountain National Park and the adjacent Estes Valley, Colorado. Elk numbers within the park were held relatively constant by management controls until 1967, after which time they were allowed to increase without human interference. Radiotelemetry of 73 elk indicated limited exchange between the subpopulations; combined with clear distinctions in population dynamics, this suggests that these subpopulations are relatively independent despite the absence of physical barriers between them. The elk subpopulation within the park initially increased at 6.5%/year between 1968 and 1970, then growth gradually slowed, exhibiting density-dependent reductions both in calf survival and recruitment with increasing population size, and approached an estimated carrying capacity of 1,069 ± 55 ($\bar{x} \pm$ SE). Since 1991, this subpopulation has remained within ±5% of this equilibrium. The adjacent Estes Valley subpopulation grew at an estimated maximum 5-year average rate of 11.0% from 1979–1983 and is still increasing at 5.2%/year (1991–2001 average). Estimated town population is currently about 70% of our projected carrying capacity of 2,869 ± 415 elk based on projection of observed calf recruitment decline with increasing population. Both carrying capacity estimates are consistent with independent estimates based on forage biomass and energy considerations. Adult cow survival rate did not differ between park and town and we estimated a constant rate of 0.913 [95% CI = 0.911, 0.915]. Bull survival rates increased in the park from 0.52 to 0.79 between 1965–2001, but remained constant at 0.42 [0.35, 0.47] in the Estes Valley. Colder winter temperatures were correlated with reduced calf recruitment (calves:cow at age 0.5 yrs) and with reduced calf survival (between age 0.5–1.5 yrs) in town. Recruitment of town elk also increased with warmer summer temperatures and greater summer precipitation. No weather covariates were significantly correlated with calf recruitment or survival in the park. Declining calf recruitment has been nearly linear and similar in both the park and town. However, density response of calf survival in the park was abrupt near carrying capacity and has not yet been detected in town, suggesting that this mechanism of density dependence is difficult to detect until the population is near carrying capacity. We estimated current combined population size of 3,049 [2759, 3369] elk in 2001. Elk in the town sector currently outnumber elk in the adjacent national park by almost 2:1 and are projected to increase by 46% before being nutritionally limited, suggesting that human-elk conflicts will likely increase in the absence of active management intervention.

Keywords: *Cervus elaphus*, density dependence, elk, national parks, natural regulation, parameter estimation, population dynamics, population models, ungulates.

---

[1]Department of Fisheries and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523
[2]U.S. Geological Survey, Midcontinent Ecological Sciences Center, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523
[3]Rocky Mountain National Park, Estes Park, Colorado 80517
[4]Department of Statistics, Colorado State University, Fort Collins, Colorado 80523

Introduction

U.S. National Park Service (NPS) policy states that natural processes should be relied upon to the greatest extent possible to regulate ungulate populations (NPS 2001). However, the policy is flexible, resulting in different management approaches in different situations. Where natural controls have been altered by human activities, unnatural concentrations of ungulates may be managed by park staff (Huff and Varley 1999). This natural regulation management of ungulates in parks has been criticized as operationally vague (Kay and Wagner 1994; Wagner et al. 1995). Olmsted (1979) and Baker et al. (1997) have attributed vegetative changes, especially declines in willow (*Salix* spp.) and aspen (*Populus tremuloides*), to high ungulate populations resulting from this policy of natural regulation. Furthermore, management targeted toward park elk may have consequences for adjacent private lands. A growing elk population located amidst a large human population has important social implications (Berris 1987). Future management in both areas requires an understanding of factors affecting population growth and regulation.

Natural regulation relies on population regulation through predator or food limitation. There is growing evidence for predator limitation of ungulates in natural systems (Bergerud et al. 1988; Boutin 1992; Gasaway et al. 1992; Messier 1994; Mech et al. 1998; Singer et al. 1998); however, uncertainty remains over the level of predator limitation in pre-European systems (Boutin 1992; Singer et al. 1997). Predators have been eliminated from many parks, and even when all predators are still present, ungulate migration patterns or habitat often have been greatly altered. Food-limited populations are assumed to result from density-dependent processes related to per capita restrictions in food availability (Caughley 1976; Fryxell 1987; Dublin et al. 1990; Choquenot 1991). Although evidence exists for food limitation of ungulates in the absence or limited abundance of large predators (Houston 1982; Choquenot 1991; Coughenour and Singer 1996; Saether et al. 1996), regulation or limitation of ungulate populations in national parks by either food or predators remains controversial (Boutin 1992; Sinclair and Arcese 1995; Boyce and Anderson 1999; Peterson 1999).

Detecting density dependence in a population from time series data is difficult. Success often requires long term-monitoring, supplemental information on survival and recruitment, and a large initial reduction (75% is suggested) by management intervention or environmental catastrophe (Shenk et al. 1998). The northern elk population in Yellowstone National Park, following release from management regulation, has exhibited considerable evidence for density dependence as periodically updated by a variety of authors (Houston 1982; Dennis and Taper 1994; Coughenour and Singer 1996; Singer et al. 1997). Similar evidence has been compiled for the Jackson Wyoming elk herd despite supplemental winter feeding (Sauer and Boyce 1983; Boyce 1989) and for red deer (*Cervus elaphus*) on the Island of Rhum (Clutton-Brock et al. 1982). Elk were similarly released from management control in Rocky Mountain National Park (RMNP) in 1968, so this population provides an independent assessment of the roles of density dependent and independent factors in elk population dynamics.

In this paper, we examine the elk that winter in the eastern portion of RMNP and the adjacent Estes Valley, which includes the town of Estes Park, Colorado (Fig. 1), referring to these sectors as "park" and "town", respectively. All of the elk in these areas are thought to have descended from a reintroduction between 1913–1914. Bear (1989) and Larkins (1997) treat these elk as a single population; nevertheless, Larkins (1997) observed that even though elk wintering in town migrated through and used some of the same ranges as park-wintering elk, they did so independently at different times. Before 1968, elk in RMNP were controlled by culling and live removal to maintain a target population of approximately 400 individuals (Stevens 1980). We focused on the period after 1967 when control of elk numbers inside RMNP ended, thereby initiating the NPS policy of natural regulation (Stevens 1980). This change in policy constitutes a >35-year management experiment on the dynamics of a population growing from an initial size well below carrying capacity (K). Elk first appeared in the town sector in noticeable numbers about between 1975–1980 (N. T. Hobbs, Colorado Division of Wildlife, personal communication), about 8–13 years after management control of elk in the park ended. Harvests of both male and female elk have been a regular part of management in town.

In our analysis, we reconsider whether distinct subpopulations exist in this area, based on telemetry locations, differences in dynamics (survival and recruitment rates), and support in our data for either temporary movement or permanent dispersal of elk. We build a series of related models with alternative parameter sets and use information theoretic model selection techniques to identify those that best explain the available data. We look for evidence of density feedback, specifically, declining population growth, calf ratios, recruitment, and survival
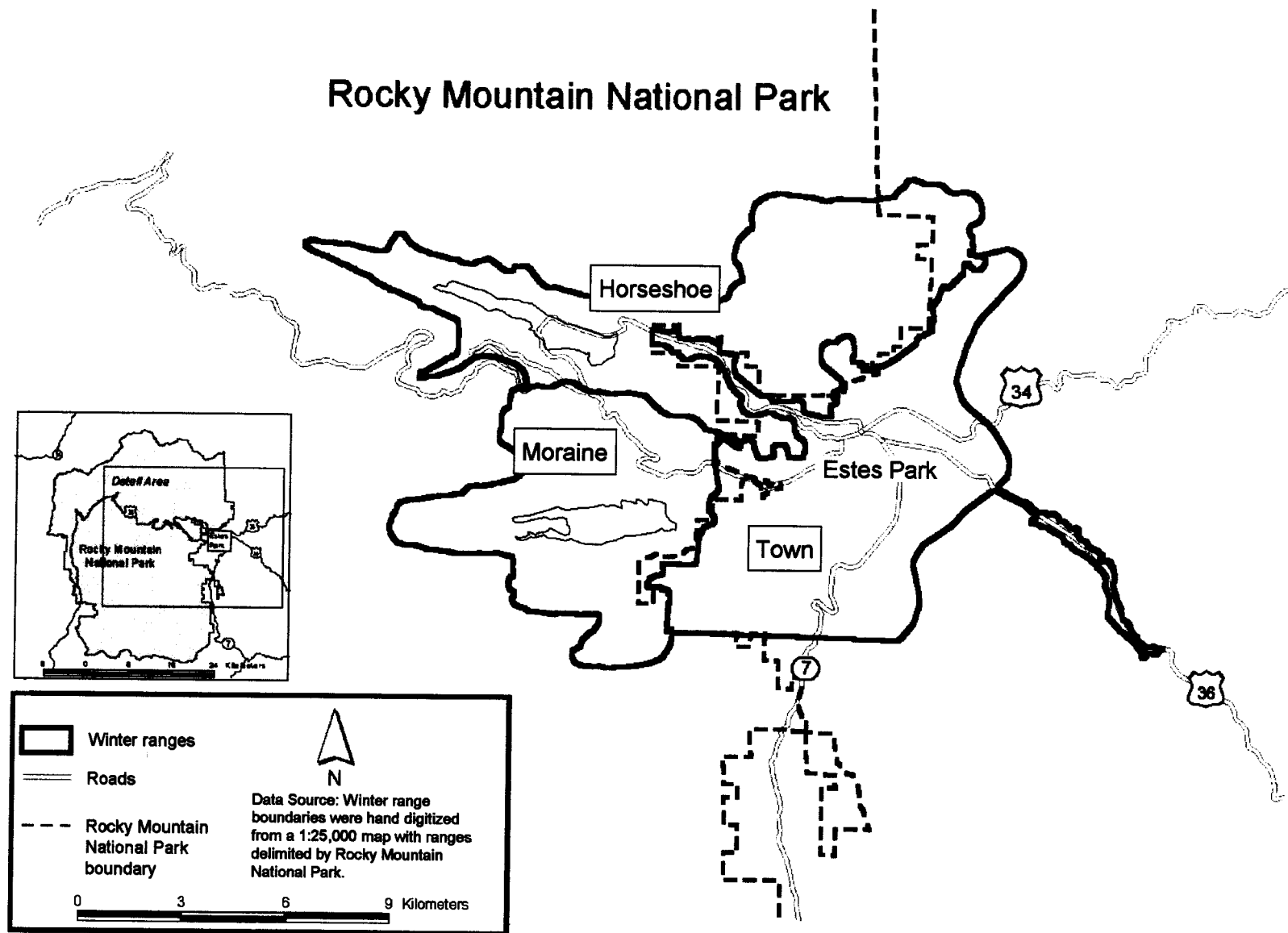
Rocky Mountain National Park

Fig. 1. Map of the study area, including the eastern portion of Rocky Mountain National Park and the Estes Valley which contains the town of Estes Park, Colorado, depicting the boundaries of three winter range areas based on all known elk locations determined by telemetry, aerial, and ground surveys. The winter range labeled "Horseshoe" also includes the Cow Creek drainage. The area labeled "Moraine" also includes Hallowell Park and Beaver Meadows.

rates inversely related to increasing elk population size. We also examine density independent correlations of calf recruitment and survival with precipitation and temperature statistics.

Methods

Several independent data sets were used in this study. Elk that winter inside RMNP have been monitored for most of this century (Packard 1947; Gysel 1959; Stevens 1980). Elk that winter in the Estes Valley outside RMNP have been monitored primarily from 1988 to the present. Elk population counts and composition data (ratios of bulls, spikes, and calves to cows) were collected in RMNP and in the Estes Valley by the Colorado Division of Wildlife (CDOW) and the NPS over the past several decades. To supplement these historical data, we collected data from 1994–2001 separately in the park and town sectors. We analyzed these multiple data sets in two phases: first we made direct estimates of population size, composition, and survival rate from the data; then we used these estimates to fit a series of alternative population projection models.

Direct Estimates

Movement and Survival

From early January through March 1995 we captured 73 elk (62 females and 11 males); each was aged, sexed, and fitted with a telemetry collar with activity monitor and an identifying tag. Elk were captured by net gun from a helicopter in the park and by dart gun from the ground in town. Elk were captured from each of the major wintering areas: 29 from the Estes Valley outside the park, 28 in Moraine Park and Beaver Meadows, and 16 in Horseshoe Park and Cow Creek. In a separate study (Larkins 1997), elk were located several times per month from the ground and fixed wing aircraft between February 1995 and November 1996. Monitoring for mortality at roughly monthly intervals continued through September 1998. Larkins (1997) provides additional details on the capture and monitoring of these elk.

We categorized all winter (defined for this analysis as November–April) locations for each elk with at least five independent telemetry locations during that period. Each elk location was assigned to one of three primary winter range areas (Fig. 1): Moraine Park (including Beaver Meadows and Hallowell Park), Horseshoe Park,

or the Estes Valley. Frequent movements of elk between Moraine Park, Beaver Meadows, and Hallowell Park within the Big Thompson River drainage indicated that these areas belong to a single winter range (hereafter referred to as Moraine). Similarly, Horseshoe Park along the Fall River combined with the Cow Creek drainage comprises a separate winter range (hereafter referred to as Horseshoe). Counts of elk locations by winter range were used to summarize patterns of winter range use and fidelity.

Survival was estimated with the known fates model in program MARK (White and Burnham 1999). Specific dates when individuals were observed alive or dead were collapsed into observations for winter (January–March), spring/summer (April–August), and fall (September–December). Alternative models with differing numbers of parameters were considered and the best of these was chosen based on AIC_c (Burnham and Anderson 1998). Annual survival rates were computed by multiplying seasonal rates; standard errors were computed using the Delta method (Cox 1998).

Park Population Size and Composition

Counts and composition data for low elevation winter range areas within RMNP east of the Continental Divide 1965–1991 were provided by Stevens (1980 and personal communication). From 1980 to 1991, ground and air (both helicopter and fixed-wing) count and classification surveys were conducted. Surveys during this time period had no specific design; instead observers attempted to find as many animals in the park as possible. Classification data for this period were not recorded by group, only total counts were recorded. Ground counts and classification surveys were conducted in 1992 and 1993 by NPS employees. From 1994 to 2001, we conducted helicopter counts and classification surveys. Classification data were recorded by group (any collection of individuals appearing to move as a discrete unit) from 1992–2001. To confirm that ground and aerial methods gave consistent classification results, we used both methods on the same day and obtained nearly identical ratios for calves per 100 cows, differing by only $1.0 \pm 3.3\%$ ($\bar{x} \pm SE$).

Helicopter surveys conducted in 1995–1998 were used to develop a sightability correction model following the methods of Samuel et al. (1987) and Steinhorst and Samuel (1989) supplemented by improved methods for variance estimation developed by Wong (1996) and implemented using PROC IML (SAS Institute 1989). The procedure does not take into account the possibility

that the counted size of observed elk groups may be in error. Counting error may result in underestimation of elk population size (Cogan and Diefenbach 1998). However, we believe this potential bias is far less severe for RMNP, because numerous and extensive open areas exist where all elk can be seen and helicopter crews slowly herded large groups of elk from areas of cover into the open before counting commenced. Nevertheless, some unknown level of undercounting bias may still be present.

These surveys yielded 44 potential sighting observations of elk groups. We assumed that the collared elk could be considered a random sample of the elk population. We used PROC LOGISTIC (SAS Institute 1990) to fit logistic regression models to the data set. Sighting characteristics considered were total group size, the natural logarithm of group size, group activity (moving or not), percent tree cover, and percent snow cover, and snow^3/10,000, following Unsworth et al. (1994). Converting percent tree cover into the seven vegetation cover classes of Unsworth et al. (1994) did not meaningfully improve results.

Town Population Size and Composition

Classification data from 1979–2001 were unpublished counts made by CDOW and NPS personnel. Aerial classification surveys using a helicopter were made in August or September of 1980–1982 in Estes Park (G. Bear, personal communication). Classification data for 1979, 1984, and 1986 are based on aerial surveys made in January of Game Management Unit (GMU) 20, which includes Estes Park, but may not represent it accurately (Steve Steinert, CDOW, personal communication). From 1988 to 2001, CDOW or NPS biologists using three to four observers conducted ground counts and classification surveys during February in the town of Estes Park (Rick Spowart, CDOW, personal communication).

To get a better population size estimate than the above counts provided, we conducted a series of 10 mark-resight surveys (Bowden and Kufeld 1995) in the Estes Valley from 1995–1997. A fixed-wing flight was made to determine the number of radio-collared elk within the count area, based on radio signal locations. Ground crews counted elk observed while traversing designated routes within the Estes Valley. Routes were selected to maximize the total number of elk seen and to avoid multiple counts of the same elk on a given day. Additionally, ground counts were made on three consecutive days within 5 days of the flight. We attempted to identify each collared elk seen using the identifying number on its collar. Elk observed in the survey area during the

ground count that had been previously classified as outside the area during the aerial survey were reclassified as available marked elk for the population estimate.

Mark-resight population estimates for 1995–1998 were developed from these data using the methods of Bowden and Kufeld (1995). These population estimates were then used as the basis for calibrating a model to estimate population size for other years based on ground count data collected during those years. This model was a linear regression of mark-resight population size estimates on the total number of elk observed during the 3-day ground count using SAS, PROC REG (SAS Institute 1990). Prediction precision was estimated for the regression. However, the residual mean square was reduced by the mean variance of the mark-resight estimates to account for this additional source of variation.

Population Composition Precision Estimates

We used a bootstrap procedure following Wong (1996:115) to compute confidence intervals for sex and age ratio estimates. Data for this analysis consisted of composition of individual elk groups sighted from 1992–2001. We generated an empirical population of elk groups using estimates of sightability based on group size, then resampled this population without replacement based on sighting probability to obtain 1,000 samples. Standard errors were computed as the standard deviation of ratios in these resampled data sets. For years lacking individual group composition data, we used the mean coefficient of variation estimated for years with adequate data, inflated by 50%. The arbitrary 50% adjustment was included to account for probable differences in methods and observers during earlier periods and served merely to place less weight on these estimates in the population model.

Supplemental Data: Weather and Harvest

Monthly precipitation and mean monthly temperature data were obtained from the weather station in Estes Park, Colorado. These data were summarized into summer (April–August) and winter (September–February) periods for use as covariates in our models of recruitment and calf survival. Harvest data were consolidated from CDOW reports and include all elk taken from Game Management Unit (GMU) 20. Unfortunately, GMU 20 encompasses a much larger area than our study and it was not possible to determine what portion of these animals were taken from the Estes Valley. Furthermore, these harvest data are based on telephone

and mail surveys, rather than check-station counts and, thus, may be unreliable. Furthermore, no measures of precision were available for harvest estimates, making their reliability difficult to assess. Consequently, we chose to estimate survival rates after all mortality sources, natural and artificial, because of the difficulty of segregating the harvest effect.

Population Models

We fit a series of alternative population projection models with varying numbers of parameters to the direct parameter estimates. Models with fewer parameters assumed that some parameters in the general model were indistinguishable and could be represented by a single value--these models represent special cases of the most general model. Some of these special cases represented important hypotheses of interests, such as whether or not park and town populations could be considered a single population or whether significant dispersal migration was occurring between them. Information theoretic methods (Burnham and Anderson 1998) were used to select the best models from this set. Effects that were supported by the data were identified by their inclusion in the best model. Models were fit for the entire time period of interest despite some missing observations, thus producing a reconstruction of the population.

Model Specification

Our models covered the period from 1965–2001 for park elk, and 1978–2001 for town elk. The Horseshoe and Moraine subpopulations within the park were pooled into a single "park" subpopulation for this analysis. The most general model considered included different parameter values for park and town subpopulations. A more general model of the elk in our study area might have allowed for separate parameters for the two subpopulations that we identified within the park (Moraine and Horseshoe). This was not done for several reasons: (1) these herds had never been considered separate subpopulations before our study and so data were previously not recorded separately for them; (2) the habitats and entire history of management of these subpopulations has been indistinguishable; and (3) calf:cow and spike:cow ratios during the period of our study were virtually identical (estimates with 95% confidence intervals in Horseshoe and Moraine, respectively, were 25.3 [21.2, 34.1] and 25.8 [21.5, 31.6] for calf:cow ratio and 4.6[1.3, 9.6] and 4.1 [2.5, 5.1] for spike:cow ratios).

Thus, pooling of data from these subpopulations for comparison to the distinctly different town subpopulation was well justified.

Each subpopulation (park and town) was modeled with five age/sex classes. Population segments were: calves (<1 year); yearling (1 < age <2) males (spikes) and females; and adult (age >2) males (bulls) and females (cows). Projections are made using a 1 year time interval referenced to the mid-winter (February–March) population survey.

Calves are recruited from the adult female segment of the population at a rate determined by a recruitment submodel and estimated sex ratio. Calf recruitment was defined as the number of calves per adult female in the mid-winter count. Calf survival was defined as the proportion of those recruited calves that survived until the following year's mid-winter count when they are reclassified as yearlings. Separate survival rates for each age and sex segment within each subpopulation were considered. Calf survival, S_c, for each subpopulation was related to local population size and four weather statistics through a logistic model:

$$\ln\left(\frac{S_c}{1 - S_c}\right) = \beta_0 + \beta_1 N_T + \beta_2 T_s + \beta_3 T_w + \beta_4 P_s + \beta_5 P_w$$

where N_T is the total subpopulation size; T_s and T_w are average summer (April–August) and winter (September–February) temperature deviations from the mean over all years of the study; P_s and P_w are average summer and winter precipitation deviations from the mean over all years of the study; and the B_i values are estimated parameters. Recruitment rate for each subpopulation was also modeled using a similar logistic function incorporating these density and weather covariates. Each winter range remained a constant size, therefore we consider correlations to population size equivalent to correlations with elk density.

With separate models for calf recruitment and survival and for both park and town populations, up to 24 parameters could be estimated for this portion of the model in the most general case. In addition, the most general model allowed for separate estimates of survival and productivity for older elk of each sex in each sector (park or town), plus a linear time trend in each of these survival rates, resulting in eight potential parameters. A common survival rate was estimated for adult and yearling males and another for adult and yearling females, because data were insufficient to distinguish these individual rates.

We included parameters to account for temporary movements of elk from one sector to the other (elk that normally wintered in one sector, but were counted in the other due to temporarily moving across the park boundary in the area of winter range overlap noted earlier). Parameters for temporary migration were only considered in years when population data were available for both sectors. We also considered permanent dispersal at either a constant rate or varying linearly with either park or town population size. All parameters were constrained to biologically meaningful values.

Parameter Estimation by Model Fitting and Selection

The specified model of elk population dynamics contained various unknown variables, some of which had been measured directly in the field and others that had not. Model-based estimates of each of the quantities observed in the field were compared to the direct estimates. Following a procedure by White and Lubow (2002), we computed a sum of squared errors between the model estimate, $\hat{\theta}_i'$, and the direct estimate, $\hat{\theta}_i$, each weighted by the variance of the direct estimate, $var(\hat{\theta}_i)$,

$$SSE = \sum_i \frac{(\hat{\theta}_i' - \hat{\theta}_i)^2}{var(\hat{\theta}_i)}$$

We used the numerical optimizing tool in the Microsoft Excel® spreadsheet software to minimize the SSE by seeking optimum values of the model parameters. Assuming normality of errors, a log-likelihood was computed from this statistic. This approach enabled disparate direct estimates, including population size, population composition, and independently estimated survival rate, to all be included in estimating an overall population model. Notice that the model estimates, $\hat{\theta}_i'$, such as population ratios, used in the least squares fit do not need to be identical to model parameters, such as survival and recruitment rates, as long as the modeled values can be used to compute estimates of the same parameters observed in the field.

We compared the ability of alternative models to represent observed dynamics using Akaike's Information Criteria with small sample bias correction (AIC$_c$) to examine the relative support in the data for different ecological parameters involved in elk population dynamics. Results are stated as AIC weights, where the best model has a weight of 1.0 to show the relative strength of support for the alternative model (Burnham and Anderson 1998).

Profile likelihood confidence intervals for the selected model parameter estimates were computed by finding the pair of parameter values (one less and one greater than the maximum likelihood estimate) that resulted in reducing the log-likelihood by 1.92 (corresponding to a 95% confidence interval) from the maximum likelihood. Estimates of precision for derived parameters (i.e., those not part of the fitted model, but computed from them, such as K) were based on the Delta method (Cox 1998). This required computation of first and second derivatives of the log-likelihood with respect to each model parameter and inverting the matrix of second partial derivatives to get the variance-covariance matrix. These derivatives and all matrix computations were computed numerically in Microsoft Excel® and Microsoft Visual Basic® using numerical methods described by Abromowitz and Stegun (1970) and Press et al. (1992).

Results

Winter Range Locations

Classification based on winter telemetry locations, placed 85% of the 73 radio-collared elk in one of the three winter ranges (Fig. 1). Of the remaining elk, 4% used both Horseshoe Park and Estes Valley ranges, 8% used both Moraine and Estes Valley, and 3% used all three. Of the 11 elk that did not use a single winter range exclusively, only one was a male. Thus, 9% of marked males and 16% of marked females were migratory. The migratory male was age 7 at capture; ages of the 10 migratory females ranged from 1–10 years. Although some individuals were observed using multiple winter ranges, none were observed to switch winter range use between years.

Elk captured in Moraine Park were observed just outside the park boundaries in an area that is also used by the town subpopulation, although not at the same time. Therefore, some elk groups could be assigned to the wrong subpopulation during counts in some years, were it not for the presence of radio-collared animals. In summary, the data suggest that there are three distinct and cohesive subpopulations of elk with different, but slightly overlapping, winter ranges with boundaries that do not correspond precisely to park boundaries.

Direct Parameter Estimates

The best model of sighting probability contains group size, activity, tree cover, and snow cover covariates.

However, in this model the coefficient for tree cover was not significant ($P = 0.125$), hence we used the simpler model without this covariate ($\Delta AIC_c = 0.575$):

$$\ln\left(\frac{u}{1-u}\right) = 2.937 - 2.506(\text{activity}) + 0.0276\left(\frac{\% \text{ snow cover}^3}{10{,}000}\right) + 0.0494\,(\text{group size})$$

where, u, is the probability of sighting a group. The model is significant ($P < 0.0001$) as are each of the slope coefficients ($P < 0.05$). Park subpopulation size estimates were made using several of the fitted sighting probability models and the Hiller 12E model of Unsworth et al. (1994). Further estimates were made for some models by applying adjustments only to groups of size less than 75. This assumed that groups of size 75 or more were always seen. All subpopulation size estimates for the same year were roughly similar regardless of which model was used (Table 1). Mean size of the park subpopulation estimates from 1995–1998 was 1,045 $\pm$ 100 ($\bar{x} \pm$ se) elk. Assuming similar sighting conditions were encountered during earlier surveys, regression of the sightability adjusted estimates versus raw counts provided a means of adjusting earlier park counts for which no covariates were available. This regression yielded:

$$\hat{N}_p = 42.442 + 1.0958\ (count)$$

Precision of estimates based on this regression was given by the standard linear regression prediction precision formula plus a 50% inflation to account for methodological differences:

$$se(\hat{N}_p) = 1.5\sqrt{2448\left(1 + \frac{1}{6} + \frac{(\text{count} - 840)^2}{211958}\right)}$$

Town subpopulation size estimates for the 11 winter survey periods between 1995–1998 ranged from 942–2,494 ($\bar{x} = 1{,}734 \pm 162$; Table 2). Some movement of elk in and out of the count area during mark-resight periods was observed, however, if collared and uncollared elk move in or out of the count area at the same rate during this time period the estimation procedure remains an unbiased estimate of the number of elk in the count area at the time of the flight to locate radio-collared elk.

Using the mark-resight estimates to calibrate the raw counts in other years yielded the following relationships:

$$\hat{N}_t = 79.82 + 0.742\ (\text{3-day count})$$

$$\hat{N}_t = 160.4 + 2.35\ (\text{1-day count})$$

The linear regression accounted for 58.3% of the variation in the mark-sight subpopulation estimates in the 3-day ground count and 79.7% in the 1-day counts. Prediction precision for these two regressions (including a 50% inflation factor for the 1-day counts) are computed as:

$$se(\hat{N}_t) = \sqrt{147455\left(1 + \frac{1}{10} + \frac{(3\_\text{day}\_\text{count} - 2195)^2}{2997580}\right)}$$

$$se(\hat{N}_t) = 1.5\sqrt{44425\left(1 + \frac{1}{4} + \frac{(1\_\text{day}\_\text{count} - 715)^2}{2170896}\right)}$$

Corrected estimates and precision are reported in Table 1.

Composition counts are listed in Table 3 along with bootstrap precision estimates for years with individual group data. Precision estimates for other years were extrapolated based on assumed coefficients of variation for park and town, respectively, of 0.575 and 0.576 for bull:cow ratios, 0.437 and 0.204 for spike:cow ratios and 0.142 and 0.088 for calf:cow ratios. Each represents a 50% inflation of the mean CV for the years with available bootstrap estimates.

Based on direct estimation with program MARK, the best AIC_c model contained no survival differences between yearling and adult age classes or between sex classes within either the park or town populations. A single annual survival rate of 0.929 $\pm$ 0.023 adequately describes the park subpopulation. Two seasonal survival rates best describe the town subpopulation: 0.821 $\pm$ 0.043 for the 7-month winter period, and 0.97 $\pm$ 0.001 for the 5-month spring/summer period. The combined annual survival rate estimate for town elk is, therefore, 0.797 $\pm$ 0.043. This direct estimate of survival represents an average of male and female survival, weighted by the proportions of each in the sample, thus this result must be compared to a similarly weighted average of the separate male and female survival rates estimated for the fitted subpopulation model.

Table 1. Elk count data and population estimates for Rocky Mountain National Park (Park) and the adjacent Estes Valley including the town of Estes Park, Colorado (Town).

Year	Park			Town			
	Count[a]	Estimate[b]	SE[c]	1 day count	3 day count	Estimate[d]	SE[e]
1965	427	510	104				
1966	437	521	103				
1967	419	502	105				
1968	310	382	117				
1969	579	677	91				
1970	419	502	105				
1971	501	591	97				
1972	589	688	90				
1973	387	467	109				
1974	516	608	96				
1975	452	538	102				
1976	863	988	80				
1977	491	580	98				
1978	812	932	80				
1979	715	826	83				
1980	739	852	82				
1981	799	918	80				
1982	689	797	84				
1983	1,387	1,562	119				
1984	809	929	80				
1985	1,010	1,149	85				
1986	750	864	81				
1987	779	896	81				
1988	854	978	80	476		1,279	357
1989	702	812	83	303		872	364
1990	753	868	81	369		1,027	361
1991	1,022	1,162	85	532		1,410	356
1992	787	905	81	557		1,469	355
1993	648	753	86	528		1,401	356
1994	552	600	34	620		1,617	354
1995	1,027	1,221	193	568	1,741	1,178	154
1996	675	788	78	552	2,477	1,727	204
1997	784	988	139	992	3,116	2,474	286

(Continued on next page)

Table 1. Concluded.

Year	Park			Town			
	Count[a]	Estimate[b]	SE[c]	1 day count	3 day count	Estimate[d]	SE[e]
1998	1,075	1,184	83	748	2,612	1,983	298
1999	932	1,036	80		3,169	2,431	457
2000	694	730	30		3,167	2,430	457
2001	1,346	1,418	56		1,754	1,381	414

[a]Counts are from helicopter surveys only in 1994–2001 and from a mixture of ground and fixed-wing aerial surveys in earlier years.

[b]Estimates are based on sightability adjustment model, described in text, for 1994–2001. Earlier years' estimates are based on a regression of estimates versus raw counts for these 8 years.

[c]Standard errors are based on Wong (1996) for 1994–2001. Earlier years' precision is based on regression prediction interval inflated by 50% to account for methodological differences.

[d]Mark-resighting survey estimates from Table 2 for date closest to the date of park estimates were used in 1995–2001. Estimates for 1994 and earlier are based on regression of 1-day counts on mark-resight estimates.

[e]Standard errors for 1995–2001 estimates are based on mark-resighting analysis. For earlier years, standard errors are based on prediction error of the regression model inflated by 50% to account for methodological differences.

Table 2. Summary of results for mark-resight population size estimates for Estes Valley including the town of Estes Park, Colorado.

Dates	Total elk count	Collared elk in town	Count of collared elk	Estimated population size	Estimated standard error	95% confidence limits
April 3–5, 1995	1,741	31	45	1,178	154.38	913–1,575
May 8–10, 1995	2,208	49	67	1,644	178.30	1,334–2,075
October 10–12, 1995	918	18	16	942	266.35	536–1,990
December 11–13, 1995	2,400	44	41	2,494	436.86	1,788–3,711
January 16–18, 1996	2,017	29	46	1,245	179.21	941–1,719
February 16–20, 1996	2,477	29	41	1,727	203.72	1,371–2,239
March 20–22, 1996	2,321	34	65	1,208	81.91	1,057–1,395
January 31–February 2, 1997	2,559	31	37	2,103	289.05	1,610–2,855
February 19–21, 1997	3,116	33	41	2,474	286.34	1,974–3,185
March 10–12, 1997	2,128	31	31	2,073	329.74	1,524–2,971
March 9–12, 1998	2,612	31	41	1,983	297.80	1,483–2,778

Table 3. Elk population age and sex composition counts for Rocky Mountain National Park (Park) and the adjacent Estes Valley including the town of Estes Park (Town), Colorado expressed as ratio per 100 cows.

Year	Park[a]						Town[b]					
	Bulls	SE	Spikes	SE	Calves	SE	Bulls	SE	Spikes	SE	Calves	SE
1965	28	16.1	13	5.5	39	5.5						
1966	11	6.3	18	7.9	53	7.5						
1967	24	13.8	9	3.9	46	6.5						
1968	33	19.0	11	4.8	38	5.4						
1969	36	20.7	9	3.9	36	5.1						
1970	12	6.9	15	6.6	26	3.7						
1971	18	10.3	14	6.1	27	3.8						
1972	26	14.9	13	5.7	44	6.3						
1973	12	6.9	13	5.7	26	3.7						
1974	15	8.6	10	4.4	39	5.5						
1975	17	9.8	17	7.4	33	4.7						
1976	9	5.2	9	3.9	30	4.3						
1977	11	6.3	11	4.8	36	5.1						
1978	11	6.3	8	3.5	35	5.0	7	4.0			60	5.3
1979							50	28.8	6	1.2	42	3.7
1980							35	20.2	6	1.2	43	3.8
1981							52	30.0	14	2.9	60	5.3
1982							35	20.2	18	3.7	46	4.1
1983												
1984			10	4.4	39	5.5						
1985			8	3.5	30	4.3						
1986			11	4.8	35	5.0						
1987			5	2.2	40	5.7						
1988			14	6.1	39	5.5	3	1.6	8	1.5	55	1.8
1989			4	1.7	34	4.8	10	5.6	10	3.4	41	2.3
1990			7	3.1	37	5.3	5	2.2	10	1.4	43	2.7
1991			9	3.9	28	4.0	6	2.7	10	3.3	37	3.2
1992	46	14.1	10	3.3	36	4.0	7	2.3	13	1.5	42	1.0
1993	31	6.2	17	5.6	56	5.4	19	6.3	13	2.0	43	3.6
1994	14	4.7	5	0.7	32	1.6	13	5.4	12	1.0	28	1.3
1995	8	2.2	6	0.8	23	1.5	15	8.6	8	1.6	27	2.4
1996	24	6.9	7	1.5	15	0.8	12	4.2	11	1.3	41	1.6
1997	9	3.0	4	0.6	30	1.2	13	1.9	10	0.5	44	1.4
1998	33	11.8	6	2.1	37	4.2	8	2.7	11	1.0	33	1.3
1999	26	21.4	3	1.6	23	2.8	8	2.5	10	0.1	31	1.7
2000	8	4.5	7	4.3	26	3.6	7	2.9	10	0.5	31	4.5
2001	20	7.4	7	0.9	26	2.5	8	3.1	8	0.8	26	1.7

[a]Composition counts for 1994–2001 were made by helicopter survey for this study. Earlier counts were made by RMNP biologists using a mixture of ground, helicopter, and fixed-wing aerial surveys. Standard errors for 1992–2001 are based on 1,000 bootstrap resamples of elk groups. Earlier estimates are assumed to have error coefficients of variation 50% larger than the average calculated for the later period.

[b]Composition counts for 1988–2001 were conducted in February on the ground using 3–4 observers, led by CDOW biologist Rick Spowart. Standard errors for 1988–2001 are based on 1,000 bootstrap resamples of elk groups. Earlier estimates are assumed to have error coefficients of variation 50% larger than the average calculated for the later period.

Population Model

The best population model fits the estimated population size data well (Fig. 2), but shows considerable deviation from the estimated population composition data (Fig. 3). In large part, this reflects low precision of the ratio estimates and the superiority of the model estimates based on inferred survival and productivity. Thus, the variation in these ratio estimates is due primarily to sampling error and not to large annual fluctuations in the actual parameters. Total population size in the park rose rapidly during roughly the first third of the study (1968–1981), then appeared to rise gradually (1982–1990) and then remain near a dynamic equilibrium during the remainder (1991–2001). Model-based estimate of population size for the town subpopulation in 2001 was 1,975 [95% CI = 1,701; 2,292] elk and 1,074 [1,000; 1,154] elk for the park subpopulation (Fig. 2).

As populations have grown over the period of study, ratios of calves:100-cows have declined in both the park and town (Fig. 3). Model-based estimates show a decline from 36.0 to 28.4 calves:100-cows in the park between 1986 and 2001 and from 50.0 to 29.9 in town between 1978 and 2001. Spike ratios have also declined steadily, from 11.7 to 6.9 spikes:100-cows in the park, and from 11.0 to 5.1 in town, over the same periods. Bull ratio changes appear to be more complex, initially falling then slowly rising in the park, while remaining steady in town; however, large measurement errors and missing values in these observations make patterns difficult to detect. However, current ratios of bulls:100 cows are substantially higher in the park (22.2) than town (6.1), presumably reflecting the differential effect of legal harvest outside the park.

Of the models evaluated, one stood out as clearly superior to all others. This best model included different values between park and town for every parameter value (Table 4) except noncalf female survival. Models that set other park and town parameter values equal, received negligible AIC_c weight (<0.1%). Removing any of the non-weather parameters from this model lowered the weight to <0.1% relative to the best model. Other combinations of the same number or fewer weather covariates were clearly inferior, receiving <5% of the best model's weight.

Male survival in both park and town subpopulations differed from each other and from noncalf female survival (Table 4). In the park, male noncalf survival rate exhibited an increasing linear trend over time from 52% in 1965 to 79% in 2001, but no trend was supported by the town data. Sex ratios at recruitment favored females

in both subpopulations, but by a larger margin in town. Calf recruitment was density dependent in both park and town, but with different slopes, reflecting the different carrying capacities of the two ranges. However, when recruitment is depicted relative to K, patterns in the park and town are nearly linear with similar slopes (Fig. 4). Calf survival differed between park and town and was negatively affected by density in the park, but not in town (Table 4). The effect of density on calf survival in the park was more abrupt than on recruitment, with about two-thirds of the reduction occurring between half of K and K. Average calf survival rates in the park and town were similar. Calf recruitment rates were unique for the subpopulations and appear to have been so throughout the period studied, however, the recruitment rates appear to be converging over time as the town subpopulation grows (Fig. 4).

Calf survival is not correlated with any of the weather covariates in the park elk. Town calf survival is correlated positively with winter temperature (Table 4). Recruitment is also positively correlated with winter temperature in the town subpopulation. Recruitment in town is also positively correlated with summer temperature and precipitation. All other weather covariate relationships tested were insufficiently supported to be included in the final model.

Evidence exists for 20 temporary cross-boundary movement events involving bulls 4 times, spikes 6 times, cows 5 times, and calves 5 times (Figs. 2 and 3). Before 2001, all temporary cross-boundary movements involved park elk being observed in the town sector, however, in 2001, calves and cows may have moved in the opposite direction for the first time. Data were insufficient to attempt estimation of temporary cross-boundary movements before 1988, so the absence of parameters from these years does not imply that it did not occur.

The park subpopulation estimates have remained within ±5% of projected K between 1991–2001 and exhibited minimal trend, increasing by only 55 animals or 0.5%/year. The town subpopulation, on the other hand, has continued to grow, averaging 5.2%/year between 1991–2001. Using parameter estimates from the best model, we extrapolated to equilibrium assuming that no significant changes in current management, including harvest regulations, occur and that male survival in the park will not continue to increase. These projections lead to estimates for $K = 1,069 \pm 55$ elk for the park and $2,869 \pm 415$ elk for town. Using estimates of winter range area from a related study (Singer et al. 2001), we computed corresponding densities at K of 10.1 elk/km² and 47.3 elk/km². Model projections predict that 90% of K will be reached in town in the year 2013.
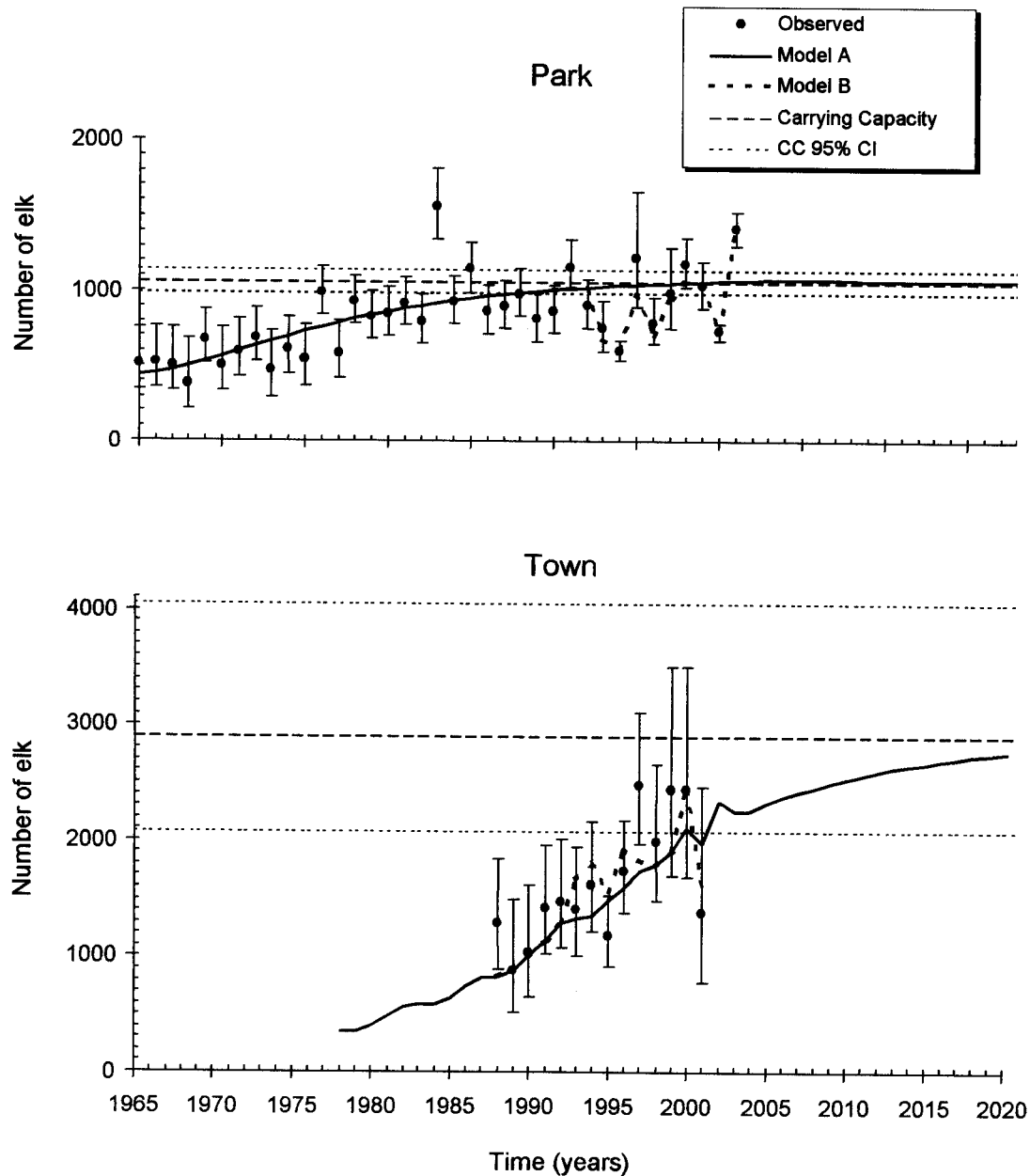
Fig. 2. Total size of elk population based on field observations and fitted models for Rocky Mountain National Park (park) and the adjacent Estes Valley, including the town of Estes Park, Colorado (town). Models include the effects of elk density, summer precipitation and temperature, and winter temperature on elk population dynamics (see Table 4 for parameter estimates). Model A depicts estimates for each actual subpopulation, Model B included the modeled effects on field estimates of 20 temporary cross-boundary movements of elk supported by the data, which resulted in miscounting some individuals belonging to the park subpopulation as town elk. Confidence intervals for population estimates are constructed from standard errors in Table 1 assuming normal errors. Ecological carrying capacity (K) is the equilibrium projected by the model with weather covariates set to their average values.
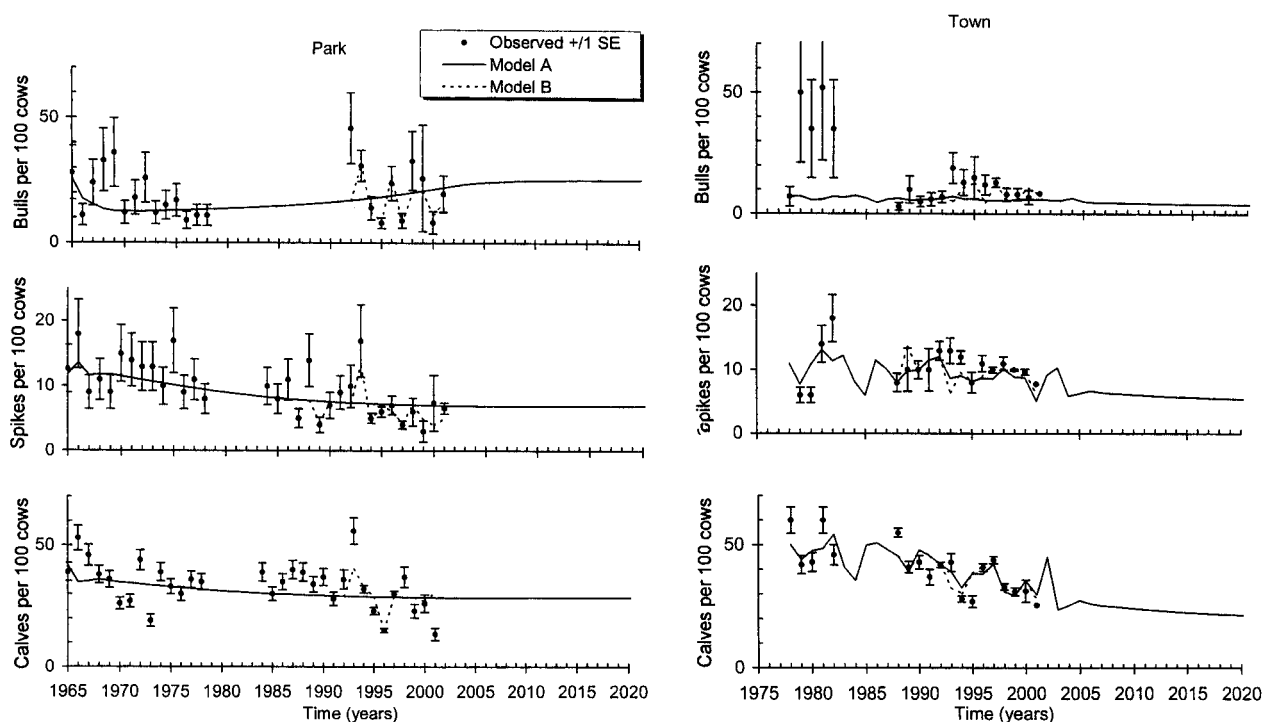
Fig. 3. Direct estimates and best fitted model for sex and age composition of elk bull:100 cow, spike:100 cow, and calf:100 cow ratios in both: (A) Rocky Mountain National Park (park); and (B) the adjacent Estes Valley including the town of Estes Park, Coloraod (town). Model A depicts estimates for each actual subpopualtion; Model B includes the modeled effects on field estimates of 20 temporary cross-boundary movements of elk that resulted in miscounting some individuals belonging to the park subpopulation as town elk. Precision of observations is shown as ±1 SE, based on values in Table 3.

Discussion

Elk were using two major migration routes during the time (1995–1996) of Larkin's (1997) study, suggesting two separate elk populations, one that wintered in Estes Valley and Horseshoe Park, and another that wintered in Moraine Park within RMNP. Timing of migrations also differed for Horseshoe Park and Estes Valley elk, confirming Bear's (1989) findings. Our reanalysis of Larkin's data confirms a strong philopatric pattern in winter range use, despite an absence of significant barriers between these winter ranges; however, we conclude that there are actually three distinct populations, based on winter range locations, and that the Horseshoe Park subpopulation is distinct from the other two.

Despite the distinct Horseshoe and Moraine subpopulations, our models pool these for the purpose of comparing them to the town subpopulation. Evidence of similar demography within the park, combined with identical management histories and habitats justify this approach. The distinctness of the town subpopulation and absence of permanent dispersal observed in the radio location data is confirmed by our population modeling. Different survival and recruitment rates can be distinguished between the park and town subpopulations, whereas dispersal migration parameters are not supported. Only recently are the calf recruitment rates of the two subpopulations beginning to converge as the town subpopulation approaches K. Thus, the town subpopulation appears to be growing independently of the park subpopulation. Although the origin of the town subpopulation was likely emigration from the park and some limited exchange may continue to take place, this mechanism does not appear to be important to its

Table 4. Parameter estimates for best (AIC$_c$) model for Rocky Mountain National Park (Park) and the town of Estes Park and surrounding Estes Valley (Town).

Parameter[a]	Park			Town		
	Estimate	LCL[b]	UCL[b]	Estimate	LCL[b]	UCL[b]
Male survival rate (age <1.5), intercept[c]	0.496	0.468	0.520	0.418	0.351	0.474
Male survival rate (age <1.5), time slope[c]	0.913	0.911	0.915	0.913	0.911	0.915
Adult (both sexes) survival rate (age >1.5)[d]	0.913	0.911	0.915	0.913	0.911	0.915
Calf survival, intercept	2.35	2.27	2.44	0.729	0.665	0.795
Calf survival, density slope	-0.00195	-0.00205	-0.00186			
Calf survival, winter temperature slope				0.392	0.337	0.449
Recruitment, intercept	0.349	0.307	0.392	0.878	0.782	0.974
Recruitment, density slope	-0.00111	-0.00115	-0.00106	-0.00074	-0.00080	-0.00068
Recruitment, winter temperature slope				0.105	0.081	0.129
Recruitment, summer temperature slope				0.261	0.238	0.284
Recruitment, summer precipitation slope				0.413	0.368	0.457
Recruitment sex ratio	0.444	0.431	0.457	0.374	0.368	0.379

[a]In addition to the 19 unique parameter estimates shown here, the best model contains 20 parameters for temporary cross-boundary movements and 2 for initial population size for a total of 41.

[b]Confidence intervals are based on profile likelihood method, i.e., parameter values are found that reduce the ln(L) by 1.92.

[c]Survival is computed as a linear function of the year, t, referenced to a base year of 1962.

[d]Common parameter for park and town.

sustained growth. This conclusion is consistent with those of Edge et al. (1986) and Van Dyke et al. (1998) who also observed strong range fidelity and herd cohesion in adjacent populations.

Although harvest data were not used in this analysis, our results are consistent with prior expectations that harvest of males should be greater for those that winter outside, rather than inside, the protection of the park. Low, but increasing, male survival in the park indicates that these individuals are also subject to harvest at some times, but that this effect has declined over time. Harvest of female elk does not appear to have a differential impact on park versus town survival rates. Many female elk that winter outside the park may remain in the park during hunting season, or, the low (1.7% from 1989–1997) female harvest rate may be too small to have a measurable effect.

An area of overlap between the Moraine and Town subpopulations observed in the telemetry data, was confirmed by the modeling which found evidence that groups of elk from the park had occasionally crossed the national park boundary and been counted in the town sector, decreasing park and increasing town population estimates in those years. Evidence for such movements exist throughout the period (1988–2001) for which adequate data are available to detect them. Given the distinct dynamics of these two populations, lack of support for models with dispersal parameters, and the absence of contradictory telemetry data, we suspect that these movements are not resulting in substantial mixing of the populations or permanent emigration from the park. Instead, it is likely that these populations do use some of the same areas outside of the park at different times, but remain demographically isolated from each other
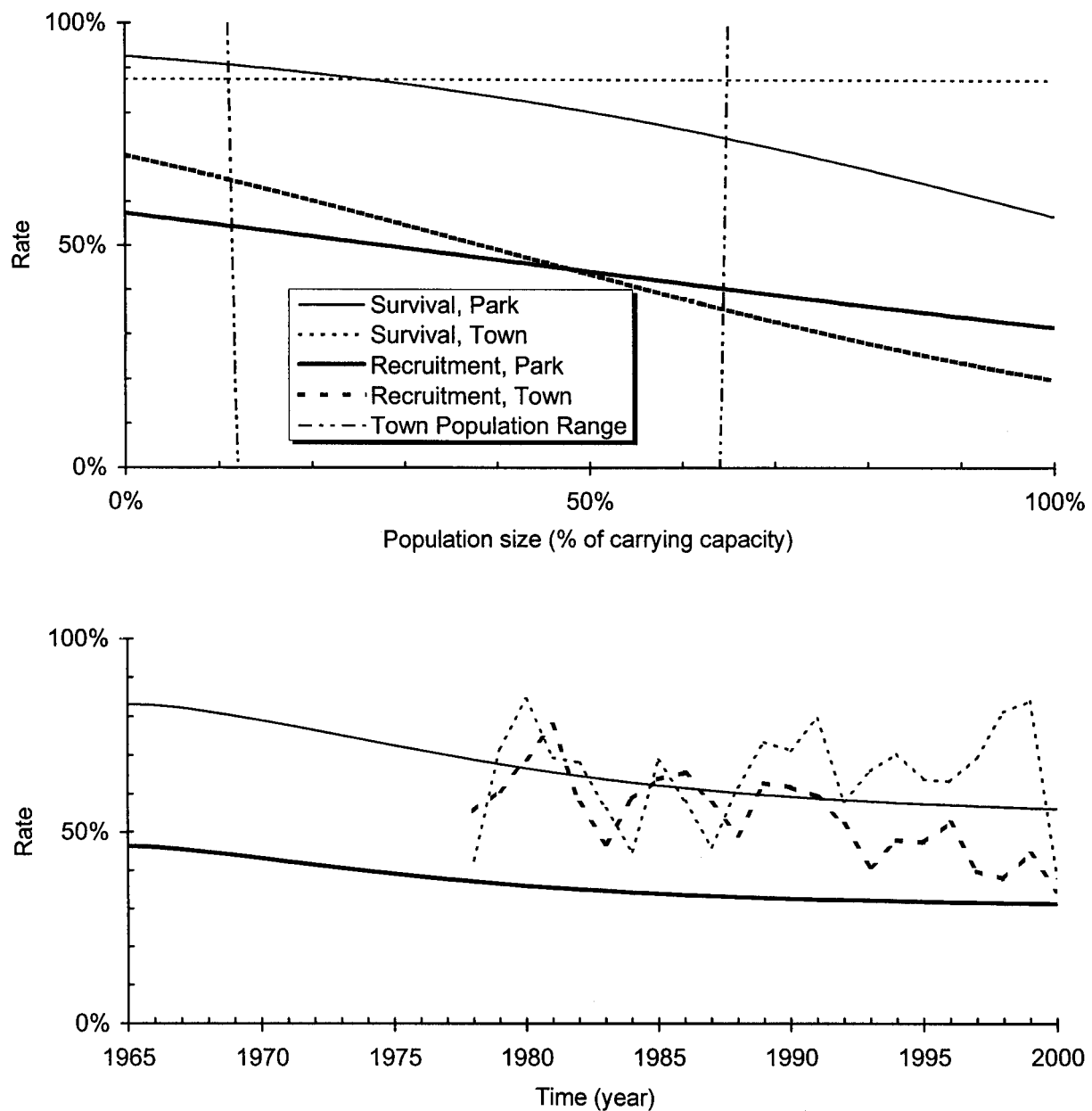
Fig. 4. Relationships between elk calf recruitment and survival rates in the park and town subpopoulations and population density relative to: (A) local carrying capacity (K) and (B) time. Relationships are based on the AIC$_c$ selected best model; however, weather covariates were set to their average values in (A) to clarify the density relationships.

through behavioral mechanisms. Until 2001, all temporary movements were from the park to town. However, the data suggest that movement from town to the park occurred in 2001. As the town population approaches K, we predict that movements in both directions will become nearly equal.

We concluded that the town subpopulation is still growing, even though the park subpopulation is no longer growing. We attribute the growth to higher recruitment and calf survival rates in town than in the park, rather than due to dispersal of elk from the park. Elk first appeared in the town sector in noticeable numbers about 1975–1980 (N. T. Hobbs, personal communication), or 8–13 years after elk in the park sector were released from artificial controls. This is also approximately the time at which population growth in the park slowed as it approached K, possibly providing the impetus for emigration. Thus, the town elk are chronologically behind the park elk subpopulation in occupying the available habitat.

Our estimated K for town assumes continuation of historic harvest levels which, so far, have not been adequate to maintain a stable population. Restrictions on hunting within town limits have undoubtedly provided the town elk subpopulation with a refuge. Our results indicate this projected equilibrium to be substantially higher than the current subpopulation size, although the projected equilibrium with continued harvest is undoubtedly lower than it would be in the absence of harvest. Thus, human-wildlife conflicts in the town, such as elk damage to ornamental shrubs, lawns, and golf courses, and potentially hazardous interactions with humans are likely to increase along with the expansion of both human and elk populations in the town sector.

We found strong evidence for density dependent feedback in the park elk subpopulation--only models that included population size feedback were supported by the AIC_c comparisons, and confidence intervals on density parameters are small. The primary mechanism of density feedback in both subpopulations was a nearly linear decline in calf recruitment, followed by more abruptly declining calf survival (Fig. 4). These mechanisms were also observed in the Yellowstone NP and Rhum examples (Clutton-Brock et al. 1982; Houston 1982; Coughenour and Singer 1996; Singer et al. 1997). Evidence for density dependence in the town subpopulation exists but is weaker, as demonstrated by the wider confidence intervals estimated for K. This is not surprising because this subpopulation has not yet reached K. The nearly linear decline in recruitment is similar to the relationship observed in the park (Fig. 4). Thus, there is no indication

that density responses of these two subpopulations are qualitatively different, just that the threshold for a detectable effect on calf survival has not yet been reached in the town subpopulation, which first exceeded half of K only as recently as 1995. Because we were unable to measure the calf survival response to density in town, it is possible that the true value of K is lower than our projections due to the effect of this additional mechanism.

The RMNP elk population example met several conditions for demonstration of density dependence that were also met in the Yellowstone NP and Isle of Rhum examples: (1) the populations were released from artificially reduced population sizes taken well below (<1/2 of) K; (2) monitoring continued for several decades until each population had reached and remained near K; and (3) total population size data was supplemented by composition data. Failures to detect density dependence (Bartmann et al. 1992; Saether et al. 1996; Shenk 1998; Smith and Anderson 1998) have involved populations fluctuating near K, used a shorter time series (<10 years), used only total population size data, exhibited high density independent variation, or were confounded by artificial feeding.

Our results indicate that both calf recruitment and subsequent survival is affected by winter temperature in town, but not in the park. Since lower temperatures are associated with lingering snow cover, it is plausible that snow accumulation in early winter reduces calf recruitment (calves first counted at age 0.5) and snow in late winter reduces subsequent calf survival (from age 0.5 to 1.5 years). Failure to detect a similar effect in the park may be due to excessive noise (unidentified sources of temporal variation or measurement error), because our earlier analysis of these same data through 1999 did detect a positive effect of winter temperature on calf survival in the park. Consistent efforts to collect snow depth data on elk winter ranges would be worthwhile and could improve our understanding of this effect.

In town, increased calf recruitment was also correlated with both increasing summer (April–August) precipitation and temperature. Both effects are likely due to nutritional effects--warm temperatures reduce the period of snow cover and more summer precipitation promotes plant growth (Sims and Singh 1978; Webb et al. 1978; Sala et al. 1988; Merrill et al. 1993). However, the park subpopulation exhibited no similar correlation. Differences between these subpopulations in the timing of migrations from winter to summer range may explain the discrepancy. Or, this may simply reflect the difficulty of detecting an effect of weather with a time series of insufficient length in an environment with only moderate

annual variation. To improve chances of discovering associations between weather and elk survival, direct estimates of calf recruitment and survival using calves captured and collared annually over long periods is required.

Our projected equilibrium K estimates for the two populations are not intended to imply that there is a single, static equilibrium for either subpopulation. Undoubtedly, changes in vegetation biomass due to variable weather patterns result in a fluctuating and possibly drifting K. Furthermore, long-term continued human alterations of the landscape in town could change carrying capacities. Since human domiciles in the town sector are currently only 30% of what is possible, (Theobold et al. 1997), we predict that human developments unusable to elk (pavement, buildings) will increase, eventually leading to reduced K for elk in the town sector. On the other hand, the annual fertilizations and irrigations of altered grasslands in the town sector may reduce annual fluctuations due to weather patterns.

The nearly 5-fold difference in absolute density of elk at K in the park and town is consistent with the analysis of forage availability. The area of grasslands in the town sector are twice as large as in the park, and many of the town's grasslands are enriched with fertilizers or irrigation (Singer et al., this volume). Thus, the forage base and potential habitat for elk in town is much larger than in the park, supporting much higher absolute elk densities. Our estimate of $K = 1,069 \pm 55$ elk in the park is remarkably close to that made >20 years ago by Hobbs et al. (1982) based on energy and nutritional considerations. Their estimates were 991 ± 102 and $1,481 \pm 261$ for a slightly dry and wet year, respectively. If carrying capacities do vary temporally as much as these results suggest, we would not expect the elk population to expand rapidly enough in good years to achieve the population size that a single year of forage availability would permit. Consequently, we expect that the observed average population would remain closer to the forage-based K imposed by poor years. The comparison of our estimate with the lower of the two estimates of Hobbs et al. (1982) suggest that this is precisely what has occurred. In a related study (Singer et al., this volume), an independent estimate of K in town, based entirely on forage biomass and quality, was $3,082 \pm 103$ elk, compared to our population projection estimate of $2,869 \pm 415$ elk. Given the substantial overlap in confidence intervals and the close agreement between these two methods for park elk, our confidence in these projections is high.

The data sets used in our analyses have been collected over several decades, by multiple investigators, and using varying methods. Consequently, the robustness of our conclusions must be evaluated in this context. Because the most reliable and consistent survey methods were used during the most recent 5 years, we lowered the weight given to earlier estimates by inflating their variance estimates. This would reduce the effect of any biases or inconsistencies on our conclusions. Although we found no undercounting of calves in the park by ground composition counts relative to aerial counts, many older males were missed by this method because they tend to forage in more densely vegetated areas. However, it is the dynamics of females that are of greatest interest in modeling a population. Furthermore, there is no noticeable discontinuity in the male composition ratios at the start of our 5-year study using aerial observations. The use of ground counts in town is less problematic because of fewer areas of dense cover and a more extensive road network. Although comparisons of absolute numbers between park and town may be biased by the survey methods, the patterns of change over time should be unaffected. Thus, the observation of continued population growth in town contrasted with relative stability in the park is not likely due to methodological differences. Nor are temporal correlations of vital rates with weather covariates in each subpopulation affected by any consistent bias. However, the differences in some estimates, such as sex ratios, could be due, in part, to such biases.

Fitting mechanistic population dynamics models to multiple sources of data is a valuable technique for extracting an understanding of a population from several noisy data sets. Although our individual data had large measurement errors, when combined with other data, reasonable estimates of vital parameters emerged. Undoubtedly, more precise data would provide better final estimates as would direct measurement of additional vital parameters, such as recruitment or calf survival. Detecting density dependence would be most easily accomplished by directly monitoring calf recruitment and survival, using radio marked calves. Because the density relationships lead to estimates of K, these would be improved as well by such data.

Management Implication

Correcting future population counts in town through our calibration relationship based on our mark-resighting estimates is undoubtedly an improvement over the raw counts. However, because of the small number of observations (11) used in developing this relationship, confidence intervals will be much wider than those for

the mark-resight estimates made in this study. Furthermore, future changes in habitat or elk behavior could bias estimates based on this calibration. Thus, we recommend repeating the mark-resighting study about once each decade.

Similarly, the sighting probability model developed for the park was developed with a limited (n = 44) number of observations. The high elevation (8,000–9,000 ft), close proximity to the Continental Divide, and frequent high winds precluded obtaining the desired number of aerial sightings, despite 4 winters of efforts. Wong (1996) recommends 300 data points to develop independent sightability models such as these. We recommend that either: (a) additional data points are gathered, perhaps from nearby drainages; or (b) these data be combined with data from other studies (Samuel et al. 1987; Unsworth et al. 1994).

Undercounting of large elk groups by as much as 20% has been documented in Pennsylvania forests, however elk groups in the open were counted without error (Cogan and Diefenbach 1998). To minimize this potential bias, we slowly herded large elk groups to the nearest opening and counted while they were standing still. Nevertheless, we recommend that future sightability studies include tests for, and estimations of, group size undercounting.

Based on this study, management actions to reduce elk population in the park might reduce the occurrence or size of occasional temporary cross-boundary movements from park to town during winter caused by elk at K seeking better foraging. However, it is unlikely that such a reduction would substantially alter the growth rate of the town subpopulation or K. The effect of harvest outside of the park on elk inside the park is uncertain. Similar survival rates in both subpopulations suggest that harvest in town may affect both, however, the harvest rate of females has been so low that an effect may not have been detectable. Sensitivity estimates from our model predict that average equilibrium population in town can be reduced by 7% by a 1% reduction in adult female survival. Thus, harvest does appear to be a useful management tool for controlling the town subpopulation, so long as restrictions to harvesting near human settlements do not interfere with harvest goals.

We estimated food-limited K for elk in the park and town sectors and these compared very favorably with independently calculated forage and energy based estimates for the same sectors (Hobbs et al. 1982; Singer et al., this volume). While potentially useful, we consider these estimations only the first step in the process of determining appropriate numbers of elk for this ecosystem. NPS policy mandates that ungulates be managed under natural processes, but two major predators (wolves and grizzly bears) have been eliminated from this system, and the remaining predators that prey on elk--coyotes and mountain lions--are very likely reduced in the developed town sector. Other studies suggest that a naturally abundant assemblage of these four native large predators would have limited elk and other large ungulate numbers somewhere below food limitation for significant periods of time (Bergerud et al. 1988; Messier 1991, 1994; Gasaway et al. 1992; Mech et al. 1998). Therefore, we suggest to park management that the elk population levels at food-limited K that we estimated here are likely higher than elk population levels defined for natural process management of ungulates in U.S. national parks (NPS 2001). Unfortunately, there is considerable disagreement over the magnitude and duration that predator limitation might take (Boutin 1992; McLaren and Peterson 1994; Sinclair and Arcese 1995; Singer et al. 1998; Boyce and Anderson 1999). We propose that Yellowstone NP offers the most similar, well-documented example of the potential limitation of elk that may occur with recovery of all native predators. Thus, the Yellowstone NP experience may provide a guide to park managers of the effect of natural processes on elk for RMNP.

Literature Cited

Abromowitz, M., and I. A. Stegun. 1970. Handbook of mathematical functions. Ninth printing. Dover Publications, New York. 1046 pp.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effect of elk on aspen in the winter range of Rocky Mountain National Park, Colorado, USA. Ecography 20:155–165.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121. 39 pp.

Bear, G. D. 1989. Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. Colorado Division of Wildlife R-S-65-89, Special Report 65.

Bergerud, A. T., W. Wyett, and J. B. Snider. 1988. The role of wolf predation in limiting a moose population. Journal of Wildlife Management 47:977–988.

Berris, C. R. 1987. Interactions of elk and residential development: Planning, design, and attitudinal considerations. Landscape Journal 6:31–41.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management 56:116–127.

Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark-sight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

Boyce, M. S. 1989. The Jackson elk herd: Intensive wildlife management in North America. Cambridge University Press. 306 pp.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone ecosystem. Pages 265–283 in Carnivores in ecosystems: The Yellowstone experience. Yale University Press, New Haven.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York. 353 pp.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 in T. H. Coaker, editor. Applied Biology. Volume I. Academic Press, New York, New York.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: Testing the food hypothesis. Ecology 72:805–813.

Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: The ecology and behavior of two sexes. University of Chicago Press, Chicago.

Cogan, R. D., and D. R. Diefenbach. 1998. Effect of undercounting and model selection on a sightability-adjustment estimation for elk. Journal of Wildlife Management 62:269–279.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573–593.

Cox, C. 1998. Delta method. Pages 1125–1127 in P. Armitage and T. Colton, editors. Encyclopedia of biostatistics. Volume 2. John Wiley & Sons. Chichester, United Kingdom.

Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: Estimates and testing. Ecological Monographs 64:205–224.

Dublin, H. T., A. R. E. Sinclair, S. Boutin, E. Anderson, M. Jago, and P. Arcese. 1990. Does competition regulate ungulate populations? Oecologia 82:283–288.

Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. Journal of Wildlife Management 50:660–663.

Fryxell, J. M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia 72:83–91.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monograph 20:1–59.

Gysel, L. W. 1959. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy- and nutrition-based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46:12–21.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. MacMillan Publishing, New York, New York.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Kay, C. E., and F. H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. Pages 151–169 in D. G. Despain, editor. Plants and their environments. National Park Service, Technical Report 93, Denver, Colo.

Larkins, K. F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. M.S. thesis, University of Northern Colorado, Greeley.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. Science 266:1555–1558.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis. 227 pp.

Merrill, E., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management 46:151–157.

Messier, F. 1991. The significance of limiting and regulation factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60:377–393.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

National Park Service. 2001. Management policies. U.S. Government Printing Office, Washington, D.C.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain

National Park. Pages 89–97 *in* M. S. Boyce and L. Hayden, editors. North American elk. University of Wyoming Press, Laramie.

Packard, F. M. 1947. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:4–12.

Peterson, R. O. 1999. Wolf-moose interaction on Isle Royale: The end of natural regulation? Ecological Applications 9:10–16.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in C: The art of scientific computing. Cambridge University Press, UK. 994 pp.

Saether, B. E., R. Anderson, O. Hjeljord, and M. Heimer. 1996. Ecological correlates of regulation variation in life history of the moose (*Alces alces*). Ecology 77:1493–1500.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys in north-central Idaho. Journal of Wildlife Management 51:622–630.

SAS Institute. 1989. SAS/IML software: usage and reference. Version 6. First edition. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 1990. SAS/STAT user's guide, Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., and M. S. Boyce. 1983. Density dependence and survival of the elk in northwestern Wyoming. Journal of Wildlife Management 47:31–37.

Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. Ecological Monographs 68:445–463.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. Journal of Ecology. 66:573–597.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predator-sensitive foraging: The Serengeti wildebeest. Ecology 76:164–173.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on calf mortality. Journal of Wildlife Management 61:12–25.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–93. Wildlife Society Bulletin 26:375–390.

Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. Journal of Wildlife Management 62:1036–1045.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park, a 10-year study. ROMO-N-13. Rocky Mountain National Park.

Theobold, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: User's manual. Second edition. Idaho Department of Fish and Game, Boise. 84 pp.

Van Dyke, F. G., W. C. Klein, and S. T. Stewart. 1998. Long-term range fidelity in Rocky Mountain elk. Journal of Wildlife Management 62:1020–1035.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C.

Webb, W. L., S. R. Szarek, W. Laurenroth, R. Kinerson, and M. Smith. 1978. Primary production and water use on native forest, grassland, and desert ecosystems. Ecology 59:1239–1247.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66(2):300–309.

Wong, C. 1996. Population size estimation using the modified Horvitz-Thompson estimator with estimated sighting probabilities. Ph.D. dissertation, Colorado State University.